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Method selection and temporal scale greatly influence ecological inferences on estimated animal behavioral states

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Abstract

Background Animal movement data are increasingly used to make ecological inferences, as well as to inform conservation and management actions. While advanced statistical methods to estimate behavioral states from these datasets have become widely available, the large number to choose from may make it difficult for practitioners to decide which method best addresses their needs. To guide decisions, we compared the behavioral state estimates and inferences from three methods (movement persistence models [MPM], hidden Markov models [HMM], and mixed-membership method for movement [M4]) when analyzing animal telemetry data. Tracks of post-breeding adult male green sea turtles (*Chelonia mydas*) were treated as an empirical example for this method comparison. The effect of temporal scale on behavioral state estimates was also investigated (at 1, 4, and 8 h time steps).

Results The HMM and M4 models produced relatively similar behavioral state estimates (compared to the MPM) and estimated anywhere from three to five states depending on the time interval of the tracks and the method used. Likewise, for all three methods, sampling movement at coarser time scales smoothed estimates of behavioral transitions. Additionally, the selection of movement metrics for analysis by the HMM and M4 also appeared to be a critical decision regarding state estimation and interpretation. At the longest time step (8 h), all three models were able to distinguish area-restricted search (ARS) behavior from migratory behavior, with greater nuance estimated by the HMM and M4 methods. By comparison, the MPM was the only model that was able to identify fine-scale behavioral patterns when analyzing the shortest time step (1 h). Moreover, the analysis of tracks with short time steps via MPM identified likely periods of resting during long-distance migration, which had only previously been hypothesized in green turtles.

Conclusions While there is no single best method to estimate behavioral states, our findings demonstrate that results can vary widely among different statistical methods and that model assumptions should be thoroughly checked during the model fitting process to reduce any potential biases. Thus, practitioners should carefully consider which methods best address their needs while also accounting for the inherent properties of their telemetry dataset.

Keywords Animal movement, Behavioral states, *Chelonia mydas*, HMM, M4, SSM, Telemetry, Time step

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Background

The collection of biotelemetry data has become increasingly common to study animal movement ecology and inform conservation efforts in recent decades [1–3]. With these datasets, researchers and conservation practitioners are often interested in what tagged animals are doing, where they can be found, and how much time they spend in a given location [4, 5]. To investigate what animals are doing when unobserved, behavioral states are estimated using one or more movement metrics that characterize an individual's trajectory [6–8]. There are a variety of methods to estimate behavioral states, where some of the most popular approaches treat the tracks as a time series during which the animal switches between two or more discrete behavioral states [8]. However, other approaches that treat behavior as a continuum may better capture complex behavioral patterns across multiple spatiotemporal scales depending on the dataset, species, and movement patterns [9, 10].

Given the wide range of methods that have been developed to estimate behavioral states, it may be unclear which method is "best" to address different questions. Ideally, study design will be question-driven, as suggested by Fieberg and Börger [11], where the questions posed will dictate which sampling design and methods should be used to address them [12]. However, sifting through the various available methods is still a laborious task given the continuous development of new methods [13]. Thus, a comparison of methods used to estimate behavioral states from biotelemetry data would benefit practitioners by guiding method selection to address their study questions while also meeting model assumptions.

Latent (i.e., unobserved) variable models that account for temporal dependence are some of the most frequently used methods to estimate behavioral states. This includes methods such as state-space models (SSMs) that often treat latent variables as continuous (although may include discrete variables or both), and a special class of SSMs called hidden Markov models (HMMs) where the latent variable is represented by a finite number of states [8, 14, 15]. SSMs and HMMs are arguably the two most commonly used behavioral state estimation methods, where SSMs are popular for marine species since they can handle location errors and irregular time intervals, and HMMs are more readily applied in terrestrial species whose data often have negligible location error and are frequently collected at regular time intervals [8]. In the analysis of error-prone animal telemetry data, SSMs are often used to account for the error structure of observations before estimating behavioral states with a subsequent model [9, 16]. Afterwards, these tracks can be analyzed by a separate state-space model that estimates a continuous behavioral parameter (such as the autocorrelation in direction and speed; i.e., move persistence), or by an HMM. To distinguish between the two state-space models, the acronym SSM will be used to refer to the model that accounts for location error while the model that estimates behavioral states will be referred to as MPM (move persistence model). Both SSMs and HMMs often assume that animal trajectories are characterized by a correlated random walk and follow a Markov process (i.e., the state at time t is only dependent on the state at time $t-1$) [8]. However, some of these assumptions may not apply to the collected data or may not properly address the questions of interest [17]. In these cases, methods such as the recently proposed mixed-membership method for movement (M4) that impose fewer assumptions while also handling missing values may provide a useful alternative [17]. Similar to HMMs, M4 estimates a set of discrete behavioral states from multiple movement metrics, but it does not rely on parametric distributions to characterize movement metric distributions and does not assume an underlying mechanistic model (e.g., a correlated random walk; [17]). Instead, M4 estimates breakpoints that segment tracks into relatively homogenous periods of movement metric values. These segments are subsequently clustered together into behavioral states, and M4 assumes that each segment may be comprised of one or more states due to the mixed-membership approach [17, 18]. Given this segment-level approach, missing values can be accommodated, but this places greater weight on observations or metrics with available data [17]. Therefore, great care is needed during study design to properly address the questions of interest.

Selecting a method to estimate behavioral states when assumptions are not met by the data may result in misleading ecological inferences [17, 19]. This requires understanding properties of the collected data and determining which (if any) processing steps should be taken to properly analyze the data by the selected model to achieve study objectives. For example, biotelemetry devices deployed on marine species typically produce irregular time series of locations that often have relatively high location error (> 1 km), whereas devices on terrestrial species often return a regular time series of positions with much lower location error (~ 30 m) [20–22]. Furthermore, selecting the number of behavioral states to be estimated from discrete state models should be based on biological knowledge of the species, the number and type of movement metrics used, as well as the temporal scale of the data. When these factors do not align with the number of behaviors to be estimated by the chosen method, practitioners may receive misleading inferences that include estimation of states with no clear interpretation or misidentification of active foraging locations [23, 24]. This is a particularly important consideration during study design since animal behavior is a continuous process that is highly scale-dependent, so the programmed time interval for the tag duty cycle will affect the number and type of behavioral states that could possibly be estimated by a given method [24–27]. The consequences of these analysis decisions could result in a misallocation of resources for conservation and management, or an incorrect understanding of how a species moves through its environment. During study design, researchers should critically evaluate what is currently known about the species of interest and determine if any previously investigated questions should be re-assessed given the advances in technology and analytical approaches.

To explore how method selection and temporal scale of telemetry data influence ecological inferences from behavioral state estimates, this study evaluated the movements of post-breeding adult male green sea turtles (*Chelonia mydas*) tracked along the coast of Brazil. These tagged individuals exhibited either migratory or range resident movement strategies, similar to many other marine and terrestrial taxa. Likewise, the same principles of (1) checking data properties against model assumptions and (2) using *a priori* knowledge of species-specific movement patterns to interpret estimated behavioral states still apply across species and movement patterns. Therefore, this green turtle case study is widely applicable to researchers within the field of movement ecology regardless of species or biotelemetry device. Specifically, this study set out to (1) compare the results and inferences from different methods (MPM, HMM, M4) used to estimate behavioral states and (2) evaluate how behavioral state estimates are influenced by the duration of the time interval separating observations. Of particular interest for our study species was the classification of migratory behavior, as well as two separate states of restricted movement (one before and the other after migration). Time intervals of 1, 4, and 8 h were compared among the different methods, which was expected to capture fine-scale daily movement patterns of green turtles (1 h), coarser movement that could distinguish between migratory and resident behavior (8 h), as well as a time step that fell in between these two (4 h). We also provide a set of recommendations to assist researchers in avoiding methods that may bias the inferences from their analyses.

Methods

Capture and tagging

Nineteen adult male green turtles were opportunistically captured (after being spotted by researchers on vessels monitoring the region) at their breeding grounds early in the breeding season (December–January) from 2019 to 2022 in the Fernando de Noronha Archipelago, which is situated 350 km off the northeastern coast of Brazil (Fig. 1, Table 1). One of these turtles (IDs 205542 and 226071) was tagged on two separate occasions, where no overlap in time existed for the transmitted locations. Captured turtles were brought to the vessel where curved carapace length (± 0.1 cm) was measured from the anterior point of the nuchal scute to the posterior tip and Inconel flipper tags (Style 681, National Band and Tag Company, Newport, KY, USA) were attached to both front flippers. After cleaning the carapace of each turtle with isopropyl alcohol, a Platform Transmitter Terminal (Argos-linked Fastloc GPS SPLASH10-F-385A, Wildlife Computers) was attached with different epoxy and fiberglass depending on the year of the project (3 M Scotch-Weld Low Odor Acrylic Adhesive DP8805NS, Devcon 5 Minute Epoxy No. 14270, Sika2 Epoxy).

Data processing and preparation

Data recorded by the Argos Fastloc-GPS tags resulted in 59,386 positions across 19 individuals. These positions were filtered to remove any anomalous points with unknown location errors before subsequent analyses. First, observations where the Argos location quality class was missing or classified as Z (i.e., did not have reported error estimates) were removed. Additionally, observations that occurred before tag deployment were removed from the dataset. Due to large time gaps (> 1 week) with intermittent observations at either the beginning or end of deployment for two tags (IDs 41587 and 41588), these leading/trailing observations were removed as well. This resulted in the removal of 29 positions in total, ultimately leaving 59,357 observations for behavioral state estimation. Tracks were visualized over space and time to ensure no additional filtering was necessary. Of these tracks, 15 individuals exhibited migration to mainland Brazil (hereafter 'migrants'; Fig. 1a), whereas five tracks from four individuals (IDs 205542 and 226071 are separate tagging occasions of the same individual) remained resident to Fernando de Noronha (hereafter 'residents'; Fig. 1b).

A continuous-time correlated random walk SSM was fitted to the raw satellite telemetry data using the `aniMotum` package (v1.2.8; [28]) in the R statistical software (v4.0.2; [29]). Location error for (Kalman filtered) Argos positions were accounted for via the reported semi-major and semi-minor error axes, as well as error ellipse orientation (i.e., the ellipsoid size and shape of the error). Error associated with Fastloc-GPS positions were accounted for using a fixed variance that was 10× smaller than the most precise Argos location class (LC 3; [16]). A speed filter of 3 m/s and a distance-angle filter to remove "spiked" trajectories (distance: 2.5–5 km; angle: 15–25°) were also applied while fitting the model to remove unlikely

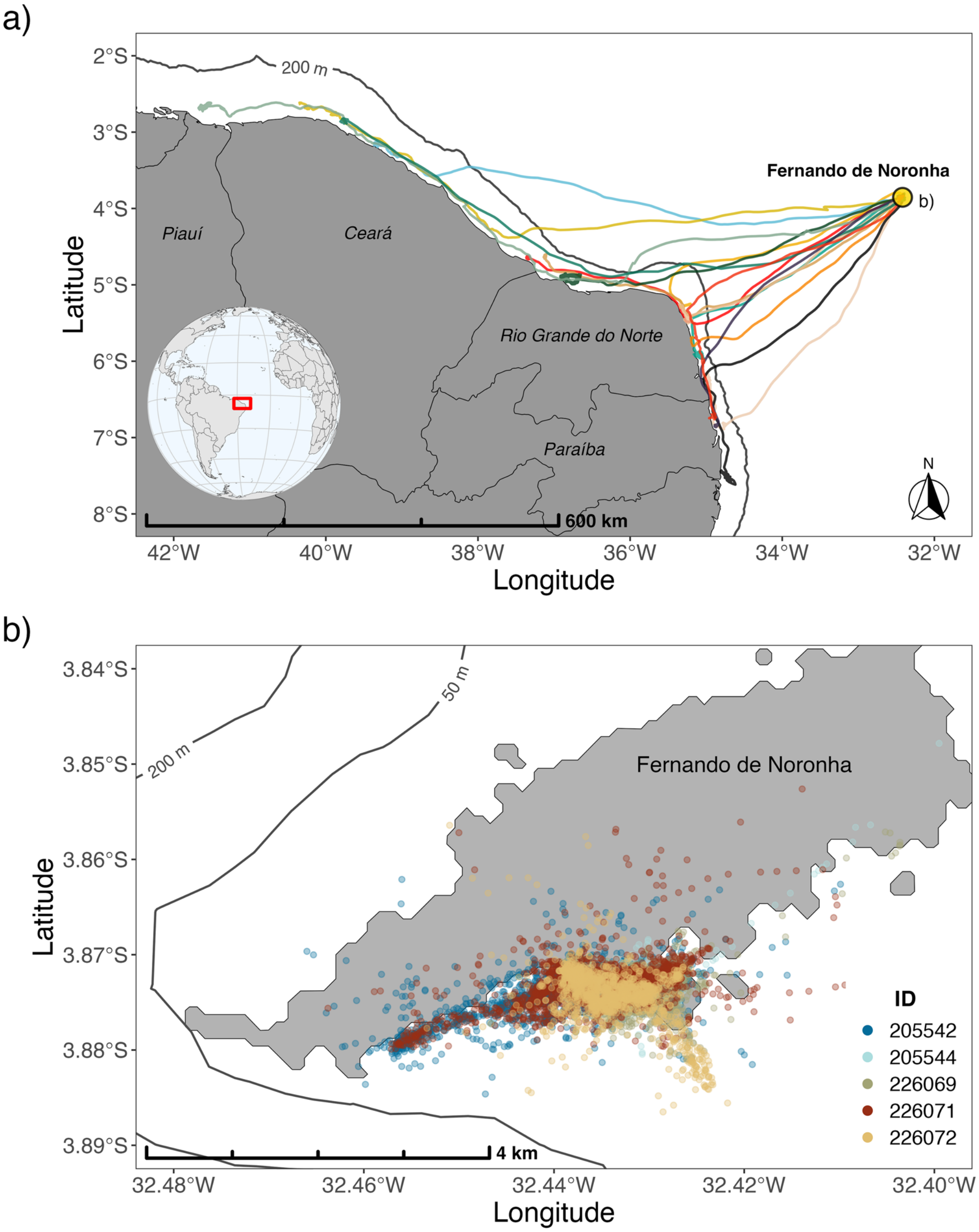

Fig. 1 Tracks of 19 adult male green turtles (*C. mydas*) tagged at Fernando de Noronha, Brazil. **a** Tracks (shown as colored lines) were processed by a continuous-time state-space model at the observed irregular time step, where the tagging location is indicated by the gold marker. The inset map denotes the extent of the study area (red box). **b** A zoomed in map of Fernando de Noronha highlights the five tracks (IDs 205542, 205544, 226069, 226071, 226072) that remained resident to the island for the duration of their tracking period

movements [16, 28, 30]. For more information on the application of SSMs to ecological time series (including animal movement data), we suggest more detailed descriptions by Auger-Méthé et al. [31], Patterson et al. [8], and Jonsen et al. [15].

The SSM was fitted at four different time steps to investigate how temporal scale may influence behavioral state inferences. This was performed at the observed irregular time step, as well as at regular intervals of 1, 4, and 8 h, where the median time step of the raw observations was approximately 1 h for each of the individual turtles. The 4 and 8 h time intervals were selected since they produced different distributions of step lengths (i.e., the distance between consecutive observations) and turning angles

Table 1 Summary data for the 19 tagged adult male green turtles from Fernando de Noronha (2019–2022)

ID	Start	End	Duration (days)	*N*			
				Irregular	1 h	4 h	8 h
195967	2019–12-16	2020–02-20	66	1273	1579	396	199
205537	2020–12-02	2021–06-08	188	4152	4521	1131	566
205538	2020–12-02	2021–02-10	70	1481	1674	420	211
205539	2020–12-29	2021–04-04	96	2099	2305	577	289
205540	2021–01-03	2021–05-09	126	2907	3034	760	381
205541	2021–01-03	2021–08-24	233	3650	5603	1402	702
205542[a]	2021–01-11	2021–07-17	187	3547	4478	1121	561
205543	2021–01-11	2021–03-27	74	1718	1782	447	224
205544	2021–01-11	2021–05-04	113	1669	2717	680	341
41588	2021–12-07	2022–03-07	90	810	2161	541	271
41614	2021–12-08	2022–04-29	142	1663	3417	855	428
41587	2021–12-26	2022–07-29	215	2619	5165	1292	647
226067	2021–12-26	2022–04-13	108	1836	2595	650	326
226068	2021–12-26	2022–05-15	140	3232	3366	843	422
226069	2022–01-11	2022–07-29	199	3809	4774	1195	598
226070	2022–01-14	2022–05-19	124	2611	2988	748	375
226071[a]	2022–01-14	2022–06-05	141	2740	3392	849	425
226072	2022–01-20	2022–07-17	178	2518	4267	1068	535
226066	2022–01-29	2022–07-04	156	3223	3746	938	470
226073	2022–01-29	2022–06-06	128	3343	3071	769	385

[a] Same individual turtle tracked on separate occasions

The ID, start date, end date, tracking duration, and sample size (*N*) for each time step are reported after tracks were processed by the state-space model

(i.e., the angle formed by two consecutive steps) while still producing multiple observations per day. Although some locations estimated by the SSM overlapped with land, these points were retained during analyses. These anomalous locations were likely a result of tag location error that could not be fully resolved by the SSM since it does not account for any barriers. For the purposes of our study on comparing behavioral state estimates across methods, we did not deem it necessary to remove these locations. However, path re-routing or data filtering when tracks cross impermeable barriers will be necessary for studies that include environmental covariates or when these sections of trajectories are expected to differ from the behavioral pattern with those anomalous points removed.

Behavioral state estimation

Three behavioral state models were fitted to the modeled tracks from the SSM to compare state estimates based on differing model assumptions. It should be noted that these tracks returned from the SSM are estimates of animal relocations based on an underlying movement model that was used to account for both location error and irregular sampling intervals. Given that the scale of movement is small compared to the location error and sampling frequency [32], SSMs that account for location error are expected to deviate from true continuous trajectories but still represent an improvement on the raw data [33–35]. An alternative approach may be to perform multiple imputation of the tracks (based on a chosen movement model) to account for location error and irregular time intervals, which also has been shown to account for uncertainty in the latent movement process [36, 37].

The selected methods included the MPM, HMM, and M4 models. Since the true behavioral states of these tagged animals are unknown, this comparison is made strictly for heuristic purposes, such as assessing whether the methods converge on similar state estimates. However, a previous comparison of HMM and M4 using simulated tracks found that the HMM outperformed M4 when tracks were generated following HMM assumptions, whereas M4 outperformed the HMM when simulations more closely follow the data-generating process of M4 [17]. Due to differences in the type of behavioral state metrics used in the three methods (e.g., the MPM analyzes animal locations to estimate a continuous behavioral metric while HMM and M4 typically analyze multiple movement metrics to estimate finite behavioral states), comparisons were made qualitatively through visualization of the results. Since the HMM and M4 methods relied on movement metrics that were time-dependent (e.g., step length, turning angle), these methods could only be used to analyze the regularized tracks resulting from the SSM (at 1, 4, and 8 h intervals). However, the MPM does not have this same constraint and was able to analyze the SSM-modeled tracks at the observed irregular time step in addition to all three regularized time steps. Although practitioners may wish to include random effects across individuals, which may improve model fit and parameter estimation while estimating inter-individual variability [38, 39], it was not included in this study to simplify the method comparison and since it could only be included in one of the three R packages used to apply the models.

A continuous behavioral state index was estimated by MPMs across all four time steps (irregular, 1, 4, 8 h) using the `aniMotum` R package (v1.2.8; [28]) after processing by the SSM (i.e., estimated separately, not jointly). This model produces estimates of time-varying movement persistence (γ), representing a behavioral continuum of slow and tortuous ($\gamma = 0$) to fast and directed ($\gamma = 1$) movement patterns. Although these values of move persistence can be directly compared across individuals for a given time step, move persistence is expected to differ in its interpretation across time steps that were analyzed. Goodness-of-fit was visually assessed using time series, autocorrelation function (ACF), and Q-Q plots of one-step-ahead residuals.

A set of HMMs were fitted separately for each of the three regularized datasets (1, 4, and 8 h time steps) from the SSM using the `momentuHMM` package (v1.5.4; [40]) in R. Step lengths and turning angles were selected as variables to estimate behavioral states, as well as net displacement (i.e., the distance of every point from the initial location) since this variable was considered to be highly informative for distinguishing migratory from restricted movements. Each of the three datasets (with different time steps) were fitted using two or three possible behavioral states, where step lengths and net displacement were assumed to arise from a gamma distribution, whereas turning angles were assumed to arise from a wrapped Cauchy distribution. Initial values for each state-dependent distribution were selected after visualizing trends in the time series for each movement variable, which varied considerably for step lengths and turning angles across the range of time steps. Visualization of estimated state-dependent distributions, mapped tracks annotated with behavioral states, goodness-of-fit via pseudo-residuals, and model comparison by AIC were used to determine whether two or three states were more likely for each dataset [24]. Each model was run 20 times to ensure that the model parameters defined the global (rather than local) maximum likelihood.

The M4 method was used to estimate behavioral states for each of the three regularized datasets by first segmenting the tracks and then clustering these segments into states using the `bayesmove` package (v0.2.2; [17]) in R. Similar to HMMs, this model analyzed time series of step lengths, turning angles, and net displacement, as well as estimated multiple discrete behavioral states. However, this model relaxes some assumptions of HMMs while simultaneously estimating the most likely number of behavioral states in a single model run (i.e., does not require model selection) [17]. Since the M4 model relies upon a categorical distribution to estimate track breakpoints as well as state-dependent distributions [17], all three movement variables were first discretized into bins prior to analysis. Due to differences in the magnitude of step lengths and turning angles at each time step, the number of bins and their cut points were slightly modified for each analysis to increase the ability of the model to identify behavioral changes (Additional file 1: Figure S1). The number of bins and the placement of cut points can be highly influential in track segmentation and characterization of state-dependent distributions (similar to the need to specify the probability density functions and initial values for an HMM). As suggested by Cullen et al. [17], the number of bins and position of bin cut points chosen should be sufficient to characterize the shape of the continuous density distribution per movement variable. This is because too few bins (e.g., < 4) may not capture the distribution well enough, and too many bins (e.g., > 10) may increase computation time and/or result in bins without any observations (which is not allowed by the model) [17]. Additionally, the position of the cut points may either be defined using a set of quantiles or using equal bin widths that span the greatest density range with a single large bin to cover the tail) [17]. For the segmentation stage of the model, 100,000 Markov chain Monte Carlo (MCMC) iterations were used to estimate breakpoint parameters with a burn-in period of 50,000 iterations and a vague Dirichlet prior, where hyperparameter α was set equal to 1. The *maximum a posteriori* (MAP) estimate of the breakpoints (i.e. the breakpoints of the model with the greatest log marginal likelihood) was then used to segment the tracks since the number and position of breakpoints can vary across models [41]. For the clustering stage of the model via Latent Dirichlet Allocation, 10,000 MCMC iterations (with a burn-in of 5000 iterations) were used and the maximum number of possible states to fit was set to 9. Vague truncated stick-breaking and Dirichlet priors were also set for the clustering model, where hyperparameters γ and α were each set to 0.1. Model convergence was assessed during both stages by inspecting trace plots of the log (marginal) likelihood. Additionally, the number of likely states were determined by a combination of the fewest number of states that represented > 90% of all behavioral state estimates on average as well as visual inspection of the state-dependent distributions for biologically interpretable states [17]. Please refer to Cullen et al. [17] and Valle et al. [42] for more details on fitting this two-stage model and the use of the truncated stick-breaking prior, respectively.

Results

The MPM estimated behavioral states as movement persistence (γ) on a continuum from slow and tortuous to fast and directed movements, which varied considerably across time steps. When examining the results at 4 and 8 h time steps (Figs. 2, 3), values of γ were low while turtles remained near the island breeding ground, followed by a brief period of high γ during the oceanic migratory period before returning to low values of γ when they settled at mainland foraging locations. At relatively short time steps (i.e., irregular, 1 h), movement persistence consistently oscillated across the full range of possible values between 0 and 1 (Fig. 3). This indicated that behavioral states constantly changed over time, spanning all types of possible movement patterns along the move persistence continuum. Migratory and resident periods were most clearly distinguished at an 8 h time step of all time steps evaluated (Figs. 2, 3). However, analysis of the tracks with an 8 h time step did not appear to capture any fine-scale movement patterns that were discerned from the other time steps, especially at the irregular and 1 h intervals. It was only at these shorter time steps that brief periods of low move persistence were detected during the migratory phase between the island and the mainland (Fig. 4). Tracks of turtles that remained resident to Fernando de Noronha (IDs 205542, 205544, 226069, 226071, 226072) were estimated to primarily exhibit high values of γ when analyzed at shorter time steps, while analysis

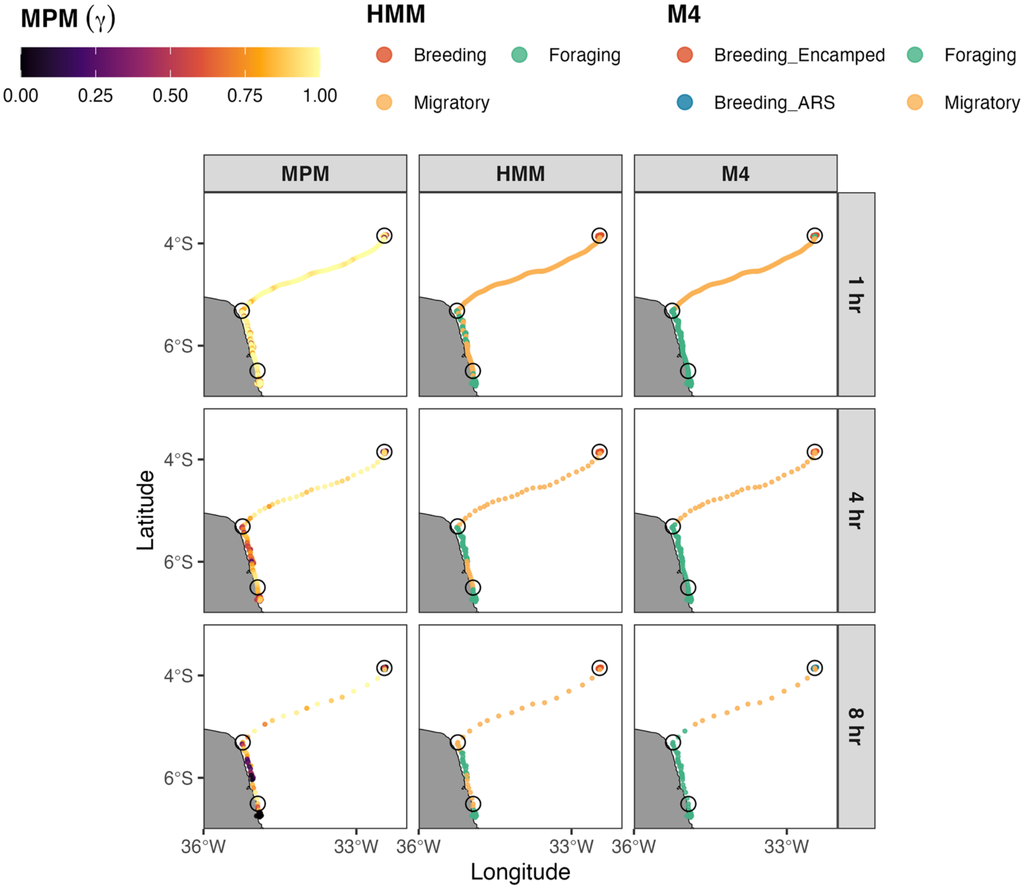

Fig. 2 Behavioral state estimates for green turtle (*C. mydas*) tracks by method and time step as shown over space. State estimates are shown for each method (MPM = move persistence model, HMM = hidden Markov model, M4 = mixed-membership method for movement) at each regularized time step (1, 4, and 8 h) for one individual (ID 41614). Colored points denote the behavioral state estimated, with a separate legend per method. The three black circles on each map correspond to the marked time points in Fig. 3, where the turtle travels from the island west across the Atlantic Ocean to the Brazilian mainland before moving south

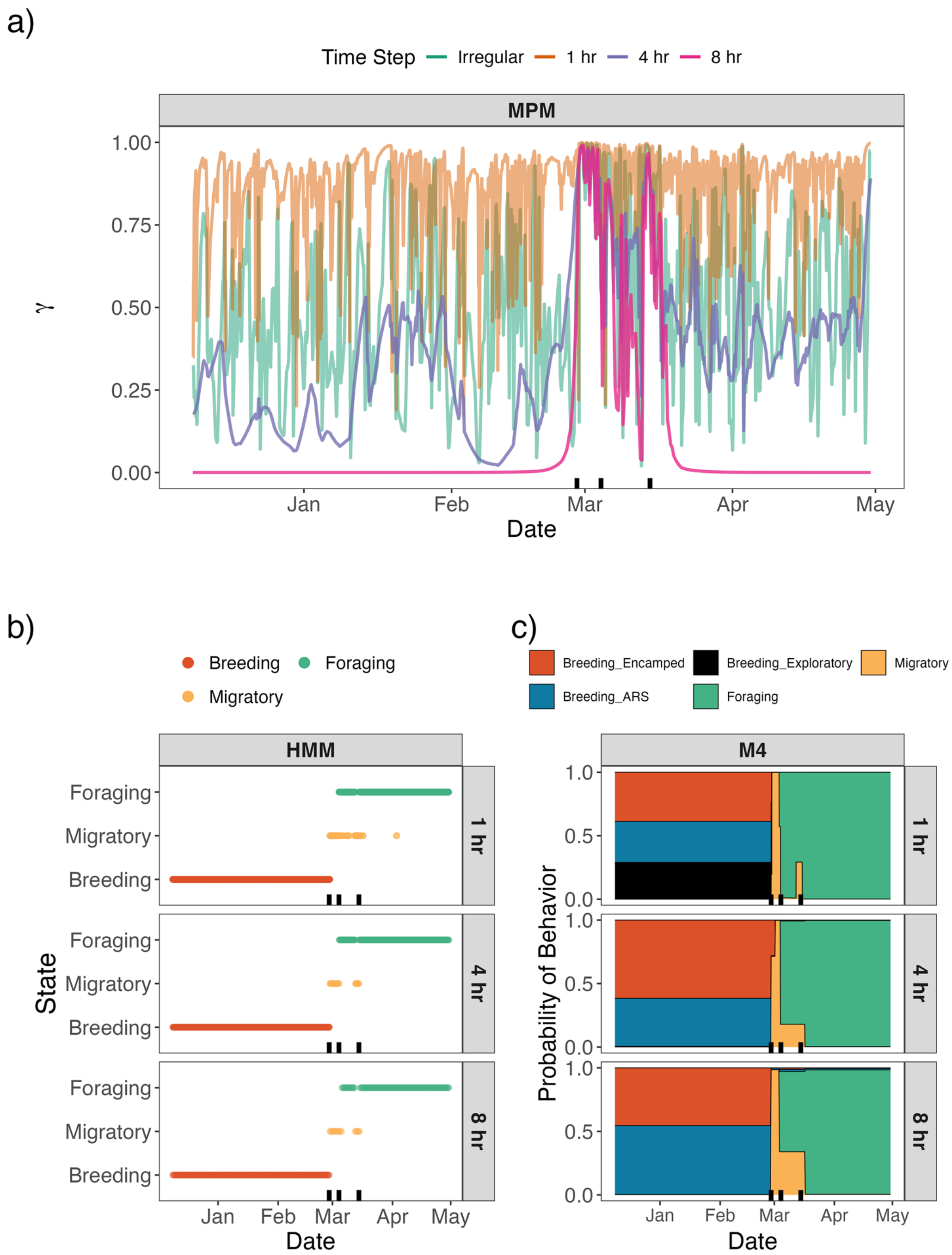

Fig. 3 Behavioral state estimates for green turtle (*C. mydas*) tracks by method and time step as shown over time. State estimates are shown for each method (MPM = move persistence model, HMM = hidden Markov model, M4 = mixed-membership method for movement) at each regularized time step (1, 4, and 8 h) and the irregular time step (only in MPM) for one individual (ID 41614). Colored lines denote different time steps for MPM, whereas colored points and polygons denote the behavioral states estimated, with a separate legend per method. Bold tick marks along the x-axis denote estimated points of state transitions, and correspond with circles surrounding points in Fig. 2

of these tracks at longer time steps resulted in primarily low values of γ that matched *a priori* expectations of restricted movement in these resident individuals (Additional file 1: Figure S2).

Across all time steps evaluated by the HMM, AIC suggested that 3 states were likely present instead of 2 states (1 h: $\Delta AIC = 32{,}980.6$; 4 h: $\Delta AIC = 9071.6$; 8 h: $\Delta AIC = 5444.8$). Based on the shapes of the

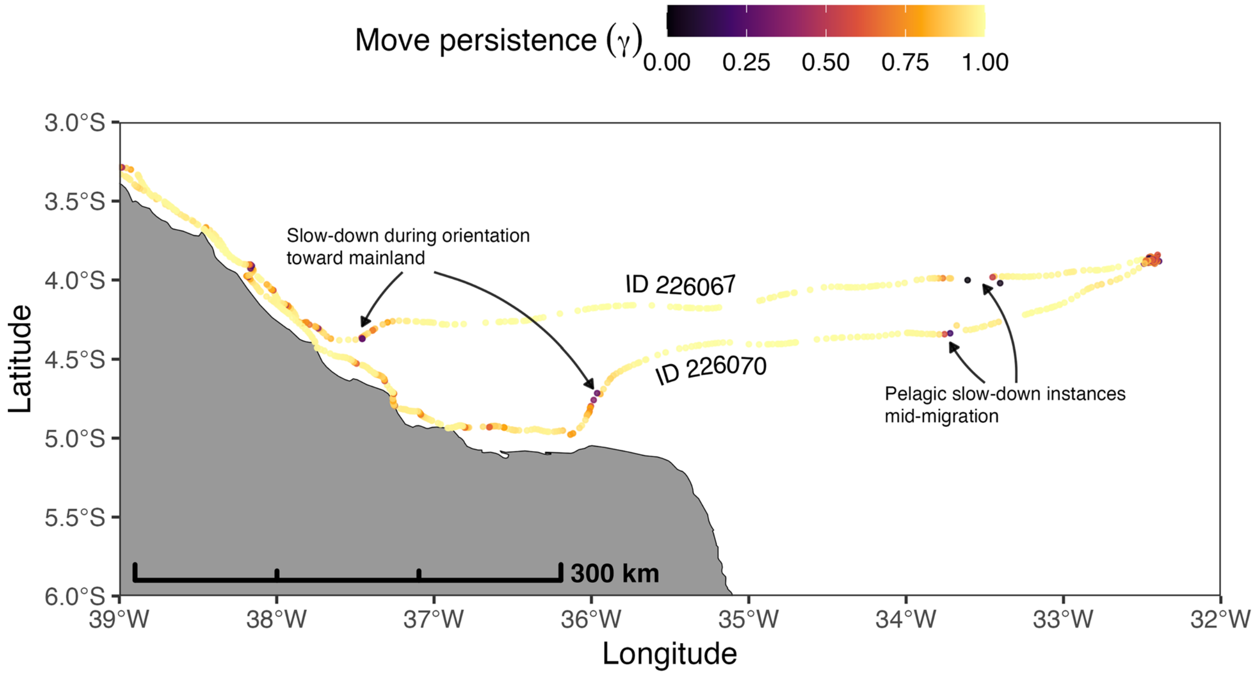

Fig. 4 Instances of low estimated move persistence mid-migration are shown at the irregular time step from the MPM. Annotated tracks for two migratory individuals (IDs 226067 and 226070) are shown in space, where colored points denote estimated move persistence. Labels mark brief periods of slower movement that may indicate a resting activity or reduced speed while navigating upon approach of the mainland

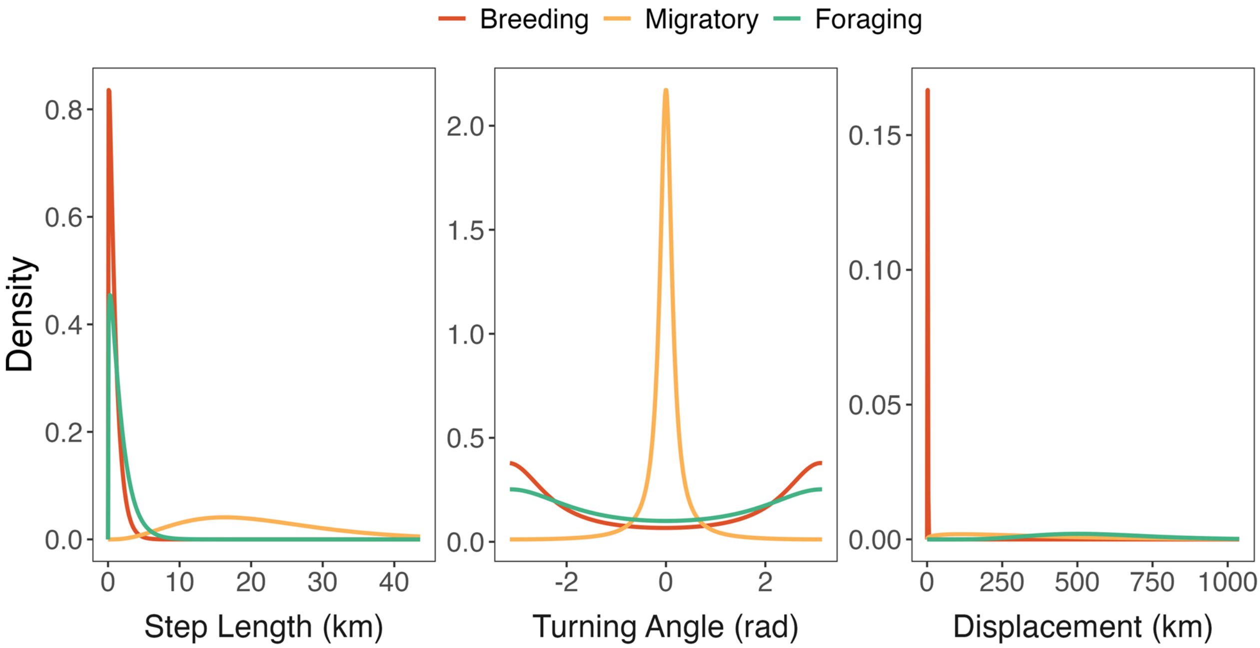

Fig. 5 Behavioral state estimates for green turtles (*C. mydas*) from the hidden Markov model. State-dependent distributions are shown for the tracks at an 8 h time step, which shows how behavioral states differ per each of the three included movement metrics

state-dependent distributions, the three estimated states were labeled as 'breeding', 'foraging', and 'migratory' (Fig. 5). The 'breeding' and 'foraging' labels indicate the location where these states occurred (e.g., the breeding site or distant foraging grounds) rather than the activity they performed since they both appeared to represent area-restricted search (ARS) behavior where the primary difference was in their distribution of net displacement (Fig. 5). Distributions for behavioral states differed across each time step since shorter time steps often resulted in shorter step lengths and turning angles closer to 0 radians (i.e., moving straight) (Additional file 1: Figure S3). In general, 'breeding' and 'foraging' states were characterized by short step lengths and large turning angles, whereas the 'migratory' state was characterized by large step lengths and small turning angles (Fig. 5). For net displacement from the breeding site at Fernando de Noronha, the 'breeding' state was characterized by small values, 'migratory' was characterized by larger values, and 'foraging' was characterized by the largest values (Fig. 5). The phenology of these identified states was supported by inspection of time series plots and maps of annotated tracks, which remained relatively consistent across time steps (Figs. 2, 3; Additional file 1: Figure S4). As was identified by the MPM, the HMM also appeared to identify rapid changes in behavior at shorter time steps compared to longer time steps (Fig. 3).

The M4 model estimated a discrete set of behavioral states from step lengths, turning angles, and net displacement (similar to HMMs), but also simultaneously estimated the number of likely behavioral states. This method estimated 4 states for tracks analyzed at 4 h and 8 h time steps, but estimated 5 likely states for tracks at a 1 h time step. To remain somewhat consistent with the naming convention from the HMM results, states were labeled as 'breeding_encamped', 'breeding_ARS', 'foraging', and 'migratory'. The fifth state of the 1 h time step analysis was labeled 'breeding_exploratory'. As with the HMM, the state-dependent distributions varied across time steps due to changes in the magnitude of step lengths and turning angles (Additional file 1: Figure S5). In general, the 'breeding_encamped' state was characterized by short and tortuous movements, which was nearly identical to the 'breeding_ARS' state that was characterized by larger step lengths (Fig. 6). The 'foraging' state resembled the 'breeding_ARS' state but possessed a multi-modal distribution of large net displacement distances (Fig. 6). The 'migratory' state was characterized by fast and directed movements with relatively large net displacement distances (Fig. 6). The 'breeding_exploratory' state (for the 1 h time step tracks) was characterized by slightly faster and straighter movements than the 'breeding_ARS' state (Additional file 1: Figure S5). The M4 model reliably estimated the phenology of behavioral states in both migratory and resident individuals, where either 'breeding_encamped', 'breeding_ARS', or 'breeding_exploratory' were likely exhibited while at Fernando de Noronha, which changed to a 'migratory' state followed by a 'foraging' state for those that traveled to mainland Brazil (Figs. 2, 3; Additional file 1: Figure S6). As with the other two methods, the M4 model also appeared to detect rapid changes in behavioral states at a 1 h time step compared to tracks regularized at a 4 h or 8 h time step (Fig. 3).

Discussion

These findings demonstrate that method selection and sampling interval of telemetry devices underlie the ecological inferences made from animal movement data, with notable differences when evaluating the MPM behavioral state estimates across different time steps. For example, individuals appeared to constantly change behavior throughout the course of a day (irregular and 1 h time steps), whereas state estimates at longer time steps (4 and 8 h) exhibited greater persistence over time and large behavioral shifts were much clearer. While the phenology of state transitions only changed slightly with increasing time step for the discrete-state models (HMM, M4), the state-dependent distributions for step length and turning angle did vary considerably; this was most notable for the change in turning angle distributions. For projects that aim to classify ARS and migratory behavior, as per this study using green turtle tracks, only HMM and M4 provided sufficient results to do so across all three regularized time steps (whereas the MPM could only do so at an 8 h time step). If instead the study objective was to classify diel behavioral patterns (at a 1 h time step), the MPM seems best-suited to address this question given its continuous state parameter (γ) that did not require the testing of different numbers of discrete states and picked up on nuances in movement persistence shifts. However, the use of more informative movement metrics at fine temporal scales may have facilitated the estimation of fine-scale behavioral states at shorter time steps. Based on these results, careful consideration should be applied when determining which method best addresses the question(s) of interest as no single method should be used in every scenario and inferences are expected to vary by temporal scale (Fig. 7).

When choosing a method to estimate behavioral states, the pros and cons of each method should be weighed in addition to an assessment of the dataset's properties (e.g., irregular vs regular time series, magnitude of location error, relative time scale of data streams, ranging vs constrained movement patterns) (Table 2). In some cases, it may even make sense to use some of these methods in combination. For example, practitioners that want to account for location error while estimating a discrete set of behavioral states may be interested in using an SSM in combination with the HMM or M4 methods (e.g., [43–45]). This two-step approach may be of particular use for Argos or light-level geolocation tags that often have

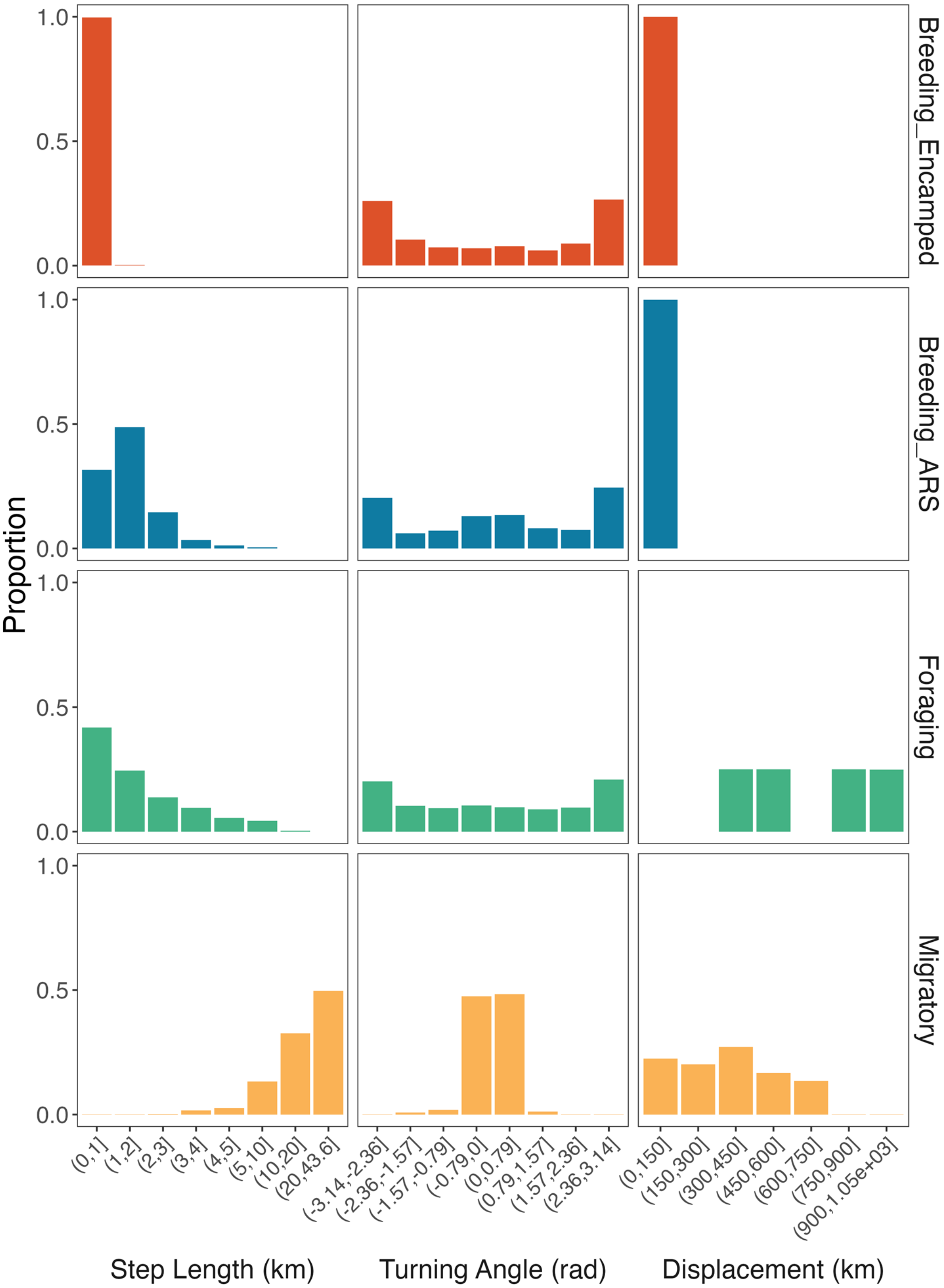

Fig. 6 Behavioral state estimates for green turtles (*C. mydas*) from the mixed-membership method for movement. State-dependent distributions are shown for the tracks at an 8 h time interval, which characterizes the estimated behavioral states across all three movement metrics analyzed

large location errors (>1 km) and exhibit irregular time steps, which frequently occurs in data of marine megafauna [16, 20]. It should also be noted that models estimating a finite number of states (i.e., HMM, M4) involve practitioners deciding which behaviors each of the states represent, requiring some *a priori* knowledge of the species to provide reliable ecological inference. However, some species may have limited behavioral data available or may exhibit movement patterns that do not readily conform to a limited number of discrete behavioral states

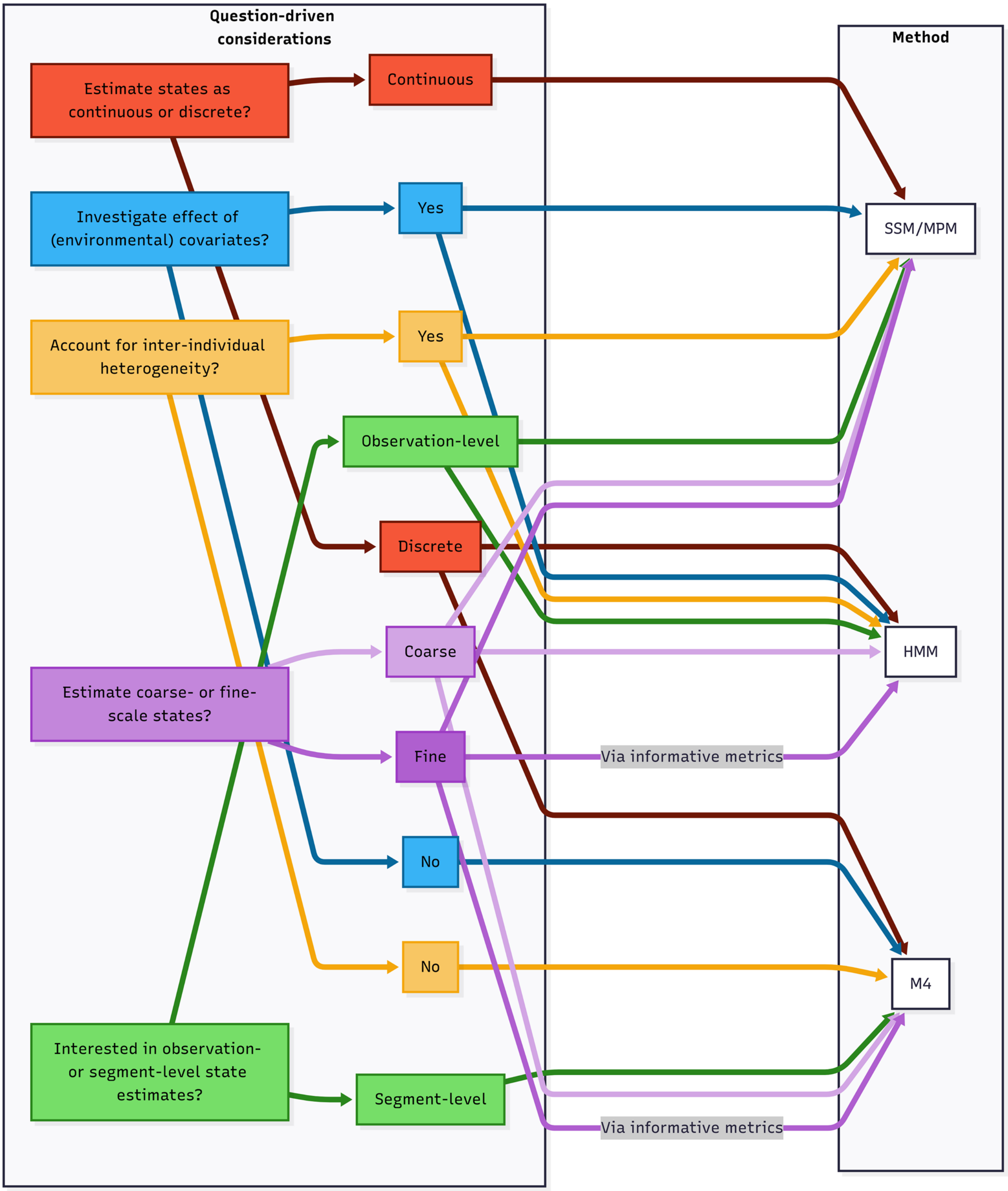

Fig. 7 A flowchart demonstrating question-driven considerations practitioners should take into account during method selection for behavioral state estimation. This flowchart provides a non-exhaustive list of common considerations facing practitioners and provides guidance on which methods may be used to address questions of interest. Colored shapes and lines are used to clarify the connections among boxes

Table 2 Guidelines for selecting methods to estimate behavioral states from animal telemetry data

Features	SSM	MPM	MPMM	HMM	M4
1. Accounts for location error	x				
2. Handles irregular time series of time-dependent metrics	x	x			
3. Assumes mechanistic movement model	x	x		x	
4. Easy to characterize > 2 states				x	x
5. Estimates states from multiple types of variables				x	x
6. Can estimate state transitions as function of covariates		x	x	x	
7. Estimates likely number of states concurrently with their distributions					x
8. Minimal model preparation and decision-making needed	x	x	x		
9. Can manually specify metrics analyzed for state estimation				x	x
10. Provides observation-level state estimates		x	x	x	

All listed features are in part reflective of the method, as well as its capabilities in the compared R packages. This comparison does not account for extensions, other R packages, or custom models that may include more features

SSM: state-space model; MPM: move persistence model; MPMM: move persistence mixed effects model; HMM: hidden Markov model; M4: mixed-membership method for movement

(especially at short time steps; i.e., < 1 h). In these cases, it may be beneficial to use the MPM (or similar SSM with a time-varying behavioral parameter) that more naturally estimates the complex behavioral continuum [9, 46]. For example, the MPM proposed by Eisaguirre et al. [10] identified a fly-and-forage behavior related to migratory pacing of actively migrating golden eagles (*Aquila chrysaetos*) by estimating behavior as a continuous parameter, which differed from the traditional stopover paradigm for migratory birds that may have been found if using a discrete-state model. If study objectives include investigating the effects of environmental covariates and/or ancillary variables (e.g., time of day, elevation/depth, temperature, distance to object of interest) on behavioral state transitions, move persistence mixed effects models (MPMMs; as *post hoc* analysis of MPMs) or HMMs may be useful since both are mechanistic models that can accommodate these types of analyses [9, 40] (Fig. 7). For example, a future study may be able to expand on these analyses by investigating how covariates such as sea surface temperature and day-of-year effect state transition probabilities, whereas support of ocean advective currents could be included as a covariate on mean step lengths. By comparison, the M4 method does not assume an underlying mechanistic movement model and provides a more data-driven approach to estimating discrete states, while concurrently estimating the likely number of behavioral states [17, 42].

Although MPMs are relatively easy to implement within the `aniMotum` R package, more effort is required when initializing the HMM and M4 approaches to estimate behavioral states. This is largely due to the importance of selecting "good" initial values for the probability density functions of each data stream or the effective discretization of data streams into bins for HMMs and M4, respectively [17, 40]. Additionally, data streams that exhibit multi-modal distributions can cause model fitting issues for HMMs. For example, the distribution of green turtle net displacement was multi-modal for the slower behavioral state of the 2-state HMM in this study, which caused issues during state estimation. This is because net displacement differed between the breeding site and foraging site (as resolved by the 3-state HMM), but also among foraging sites as well, and could not be properly estimated by parametric distributions. Therefore, only step lengths and turning angles were analyzed in the 2-state HMMs.

The temporal scale (i.e., sampling interval) of the telemetry data exhibited a large impact on the estimated behavioral states across all three methods compared. The shortest regularized time step evaluated by this study (1 h) suggested high movement persistence (MPM), rapid changes in behavioral state (HMM, M4), and even the detection of an additional behavioral state beyond those estimated at the 4 and 8 h time intervals (M4). However, the tracks regularized at the 4 and 8 h intervals converged on very similar behavioral states that were more reflective of the coarser patterns exhibited over larger spatiotemporal scales. Since high frequency biotelemetry data exhibit a high level of autocorrelation, the M4 method may provide more accurate behavioral state estimates than HMMs when state dwell times (i.e., the time spent within a state) do not follow a geometric distribution [24]. However, a hidden semi-Markov model relaxes this assumption by directly modeling dwell times per state and may be a suitable alternative [47, 48]; this type of model can be implemented in R packages such as `hsmm`, `PHSMM`, or `LaMa` [49–51].

Since all three models were able to detect different behavioral patterns across the temporal scales evaluated, it appears that there was a signal in the data they were each able to detect. Therefore, shorter time intervals facilitate the estimation of a greater number of states at a finer resolution than is possible at longer time intervals. At very short time intervals (i.e., < 1 s to 5 min), most step lengths are expected to be quite short and turning angles will be mostly straight, making the use of these two metrics alone more difficult to distinguish and interpret a set of finite states from HMM or M4 compared to the continuous move persistence metric of the MPM. However, the use of other metrics (particularly from an accelerometer or other on-board sensor) in addition to standard step length and turning angle metrics are likely necessary to estimate informative behavioral states at fine temporal scales. By comparison, most existing methods were developed to analyze relatively coarser temporal scales (i.e., > 1 h), so the use of step lengths and turning angles alone will be more informative to models such as HMM and M4 while MPM is expected to estimate behavioral patterns at a coarser resolution.

Given the rapid advances in biotelemetry devices that have facilitated data collection on the scale of minutes to seconds, the analysis of fine-scale biotelemetry data will become even more common and require increasing consideration by practitioners [52]. One such example includes the analysis of data streams collected at different time scales (e.g., accelerometer [Hz] and GPS data [min]), which can be jointly used to estimate behavioral states via hierarchical HMMs [53, 54]. Depending on the study questions, data streams analyzed, and expected behaviors of interest, the data may need to be summarized or coarsened to improve behavioral state estimation if this is not possible at the observed sampling interval. Alternatively, the use of first-passage time [55] could be used to investigate the scales of ARS behavior, or the appropriate scale could be “extracted” if analyzing big data [56].

While all three methods were able to distinguish ARS from migratory behavior at the coarsest temporal resolution (8 h) and rapid behavioral shifts at fine time intervals (1 h), each of the methods provided nuanced differences in behavioral inference for this particular analysis. Although the MPM estimated behavior as a single parameter (movement persistence), which did not force behaviors to fit into a set of discrete states, it may also be more difficult to interpret what the animal is doing at intermediate values (i.e., 0.25–0.75) based on this derived metric. Additionally, the MPM (fitted in `aniMotum`) did not allow behavioral state estimation based on a set of user-selected movement metrics (but see [10, 57] for examples that include covariates). However, the use of a continuous behavioral state at fine temporal scales (1 h, irregular) was much more adept at estimating fine-scale behavioral patterns that were not identified by the discrete-state models.

By comparison, the HMM estimated three behavioral states for each time step analyzed, but that was only because a maximum of three were estimated and expected *a priori*. Therefore, it is possible that more behavioral states could have been identified if we tested a greater number of states. For this analysis, the HMM was able to successfully discriminate migratory movement from ARS behavior (at the island or mainland), including brief periods of migratory movement as turtles reached the mainland and moved along the coastline before settling in foraging habitat. These patterns are consistent with those of post-nesting adult females that may (or may not) undertake long-distance migrations and settle at coastal foraging grounds where they display limited movements [58–60]. Since we did not test greater than three states and used certain movement metrics that were intended to distinguish coarser behavioral patterns (e.g., net displacement), fine-scale behavioral states were not identified. Therefore, HMMs are more likely to provide better estimates for a set of expected behavioral states (in number and distribution) compared to a set of unexpected states for a species with limited existing information on movement patterns. However, this also appears to be highly dependent on temporal scale.

State-dependent distributions from M4 resembled those of the HMM despite discretizing movement metrics into bins. One large difference in estimates from this method was that the period that turtles spent at Fernando de Noronha was often estimated as a combination of multiple behavioral states (e.g., breeding_encamped, breeding_ARS, breeding_exploratory). This provided slightly greater nuance than what was provided by the HMM or MPM. Likewise, the entire track segment after migratory individuals reached the mainland was primarily classified as foraging behavior, although brief periods with some proportion of migratory behavior was estimated after individuals reached the mainland. When annotating tracks based on the dominant behavioral state, this nuance was not readily visible; only when tracks were annotated via the proportion of a given state was this clearer. Based on these findings, it seems that these brief periods of behavioral shifts were easier to identify from MPM or HMM estimates. But unlike the HMM, M4 estimated 5 likely behavioral states at a 1 h time step. While this method had the capacity to do so, it is not clear that this necessarily changes the interpretation of the results given that the movement metrics analyzed were better for characterizing migratory from non-migratory movement rather than fine-scale behavioral patterns (as was found for the HMM). Therefore, we found that movement metric selection (in addition to number of metrics) is also critical to making inferences on behavioral patterns beyond only estimating a greater number of different states.

Green turtles often exhibit high site fidelity during much of the year, moving relatively short distances once they have settled in suitable foraging habitat [58, 61, 62]. Additionally, previous studies have typically only estimated behavioral states as 'ARS' or 'transit' based on changes in location (e.g., [59, 63–65]) using an earlier 2-state SSM for animal movement [66]. Results from the analysis of step lengths, turning angles, and net displacement in this study demonstrated that the HMM and M4 methods were able to successfully estimate multiple discrete states as characterized by a set of state-dependent distributions that were used to infer what these turtles were doing. The M4 approach was able to distinguish between movements where turtles were possibly resting or foraging within a single location (breeding_encamped; step length < 1 km for $t = 8$ h) and slightly larger but restricted movements to find food or mates while at the breeding location (breeding_ARS; step length primarily between 1 and 2 km for $t = 8$ h). These results provide initial findings on the behavioral complexity of adult male green turtles, which appear to resemble that of post-nesting adult females. This behavioral analysis could be expanded further by including environmental covariates on the transitions among states, as well as focusing more directly on fine-scale behavioral patterns using the 1 h time step and selecting movement metrics that may better capture these differences (e.g., step length, turning angle, dive depth and duration, distance to shore). In this study, the MPM identified low movement persistence intermittently throughout the migratory period for some individuals when analyzed at 1 h or the original irregular time step. It appears that these long-distance migrants slow down (if not briefly rest) during their journey to foraging grounds at the mainland, which corroborates findings in migrating loggerhead sea turtles [67] but has not been thoroughly investigated in green turtles (but see [68, 69] for suggested diel patterns related to diving activity during migration). Given the complex range of coarse- and fine-scale patterns exhibited by these green turtles that are also observed in many marine and terrestrial species, this comparative analysis demonstrates the relative performance among these tested methods and subsequently provides guidance that is widely applicable to movement ecology studies.

Conclusions

As studies of animal movement are increasingly used to inform conservation and management plans [70–72], it is critical that the estimates used in decision making are as accurate as possible. Since there is no single best method for all possible applications or studies, researchers should carefully consider how a given method could be used to address their questions of interest and ensure that the model assumptions are met. Moreover, the selection of methods simply because they have been frequently used by previous studies (and not because they best address the questions at hand given the properties of the data) are strongly discouraged as these results are likely to exhibit a high level of bias. Although SSM/MPM and HMM are the most common models used to analyze data from marine and terrestrial species, respectively, models that are more data-driven (such as M4 or machine learning methods) have also proven useful as suitable alternatives. Given the recent development of statistical methods that can accommodate multiple biotelemetry data streams, environmental covariates, random effects, and temporal autocorrelation, researchers can even begin to reanalyze previously collected datasets to either validate earlier findings or update the current state of knowledge on the species of interest. Greater critical consideration of temporal scale and method selection for estimation of behavioral states from animal telemetry data will therefore be of great benefit in providing ecological inferences with reduced bias.

Supplementary Information

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Additional file 1: Supplementary figures

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Author contributions

JAC and MMPBF conceived the ideas and designed methodology; MMPBF, JWW, LMK, and GS performed project administration; AJBS collected the data; GS provided resources at the study location; JAC analyzed the data; JAC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Availability of data and materials

Data and code supporting this research are available in the following Zenodo repository: https://doi.org/10.5281/zenodo.10476175.

Declarations

Ethics approval and consent to participate

Animal capture and tagging protocols were approved by Institutional Animal Care and Use Committee permits from Florida State University (#s 1803 and

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Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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